LIFE CYCLES, MATING, AND COLOR CHANGE IN TORTOISE BEETLES (COLEOPTERA:CHRYSOMELIDAE:CASSIDINAE)

EDWARD M. BARROWS

Department of Biology, Georgetown University, Washington, DC 20057,
and The University of Michigan Biological Station, Pellston, MI 49769

ABSTRACT

In the laboratory, *Deloyala guttata* and *Metriona bicolor* develop from eggs to adults in from 23 to 43 days. Their larvae and those of *Plagiometriona clavata* construct and carry fecal masses that appear defensive in function. Adult *D. guttata* and *M. bicolor* usually attain full metallic coloration when they are from 9 to 27 days old. Copulation usually occurs with the male mounted on the female, and it lasts from 15 to 583 min. Beetles often copulate repeatedly with the same mates and are also polygamous. During copulation, older adults of *M. bicolor* change color in from 120 to 1033 sec from brownish orange with black spots to brilliant, metallic gold. These beetles are usually gold when they are undisturbed. Disturbance causes them to turn from gold to goldish orange with black spots in from 12 to 141 sec and then eventually to turn to brownish orange with spots. While changing color, males show spots significantly faster than females. Possible adaptive reasons for rapid color change in *M. bicolor* are discussed.

INTRODUCTION

Various aspects of the biologies of North American tortoise beetles have been reported (e.g., Walsh and Riley 1869; Swain 1948; Smith 1950; Shell 1964; Woodruff 1965, 1975, 1976a, b; Eisner *et al.* 1967; Beshear 1969; Balsbaugh and Hays 1972; Ward and Pienkowski 1976; and Jackman 1976). This study reveals some previously unreported information about tortoise beetles, and it concerns *Deloyala guttata* (Oliv.), *Metriona bicolor* (F.), and *Plagiometriona clavata* (F.). *D. guttata* is found from Eastern United States to South America; *M. bicolor,* Eastern United States; and *P. clavata,* Eastern, Central, and Southwestern United States (Leng 1920; Woodruff 1975, 1976b). *M. bicolor* is sometimes an economically important pest of the sweet potato, *Ipomoea batatas* (L.) Lam. (Convolvulaceae). Adult cassidines may be unique among insects because of their ability to reversibly change their structural, metallic colors. Quick, reversible color change is also found in acridids *Kosciuscola* spp. which employ pigment movement (Key and Day 1954a, b; Filshie *et al.* 1975). *M. bicolor* often undergoes rapid color change during copulation as is reported below; to my knowledge, this is the first record of such behavior in insects.

MATERIALS AND METHODS

Tortoise beetles were collected in 1976 from their food plants in Washington, D.C. *Deloyala guttata* and *Metriona bicolor* were collected from

Calystegia sepium L. and *Ipomoea purpurea* (L.) Roth (Convolvulaceae), and *Plagiometriona clavata* were collected from *Datura stramonium* L. (Solanaceae). In the laboratory, beetles were maintained or reared in petri dishes in which fresh leaf pieces were placed every 1 or 2 days. Beetles were maintained under a natural photoperiod and illumination by indirect sunlight at from 23 to 27°C. Beetle sexes were ascertained by watching their sexual behavior. Males were marked on their scuta with fast drying enamel paints after they copulated or after they extended their aedeagi, and females were marked after they copulated. Behavior was timed with a stopwatch. "N" designates sample size; MWUT, Mann-Whitney U-test. Numbers in parentheses which follow ranges represent mean, one standard deviation, and median, respectively. For convenience, some methods are given in the Results and Discussion.

Results and Discussion

Life histories. Adults of *M. bicolor* were found in the field from early May to early October; *D. guttata* and *P. clavata,* from June to September. In the laboratory, 32 eggs of *M. bicolor* hatched in from 5 to 8 days (7.4, 1.13, 8.0); 33 eggs of *D. guttata,* 2 to 7 days (5.3, 2.41, 7.0). Female *D. guttata* usually defecated on their oothecae as do females of other tortoise beetles, e.g., *Cassida hemisphaerica* Herbst (Maw 1976); perhaps this somehow protects oothecae. Twenty six larvae of *M. bicolor* took from 21 to 25 days (21.7, 1.01, 22.0) to reach pupation age; 13 larvae of *D. guttata,* 18 to 23 days (22.2, 1.88, 23.0). Two hundred and twenty three pupae of *M. bicolor* became adults in from 6 to 9 days (6.9, 0.59, 7.0); 55 pupae of *D. guttata,* 3 to 9 days (4.7, 1.31, 5.0). Smith (1950, p. 101) reported different *M. bicolor* life cycle durations, possibly because he observed these beetles in a different part of the U.S. and under different conditions.

Larvae carry masses of exuviae and feces over their dorsa with use of abdominal urogomphi (Fig. 1). Larvae of *M. bicolor* and *P. clavata* carry single large masses; whereas, larvae of *D. guttata* each often carry from one to four masses that are loosely joined. One larva of *D. guttata* extended and bent its abdominal end over its dorsum so that its end reached about three-fourths of the way to its head and it defecated on both sides of its mass. Larvae of *M. bicolor* were observed to defecate on one or the other side of their masses, but the symmetry of their masses suggests that they defecate on both sides at about the same frequency.

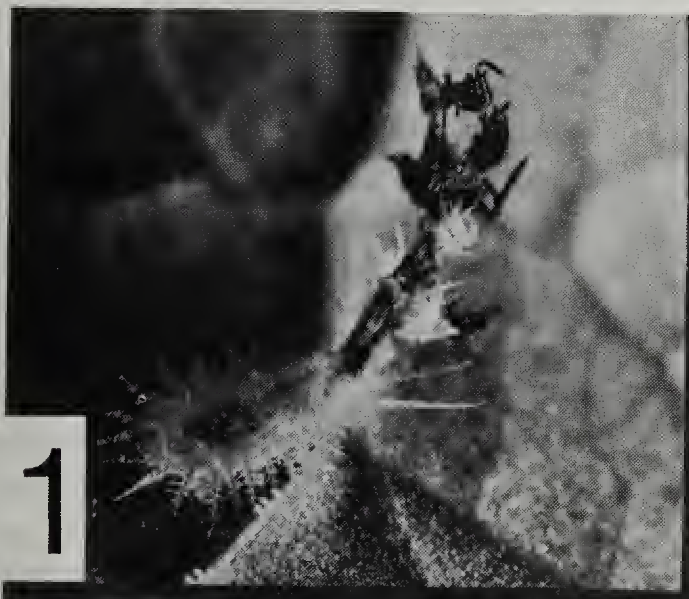
Larvae move masses with their urogomphi over areas of their bodies which are tactually stimulated. Medium-sized larvae were touched on their anteriors, posteriors, and both sides with a blunt, carbon tip of a pencil. Typical larval response was to move their masses so as to cover and, thus, apparently defend areas that were touched. Ten larvae of *M. bicolor* and 9 out of 10 larvae of *D. guttata* that were all from different parents showed typical responses. Also, 8 larvae of *P. clavata,* not all from different parents, showed typical responses. Eisner *et al.* (1967) found that in *Cassida rubiginosa* Müller, larval masses ("shields") are highly effective in blocking ant bites, and they also mention other possible functions of masses such as camouflage and protection against desiccation or rain. Functions of masses in other cassidines require study.

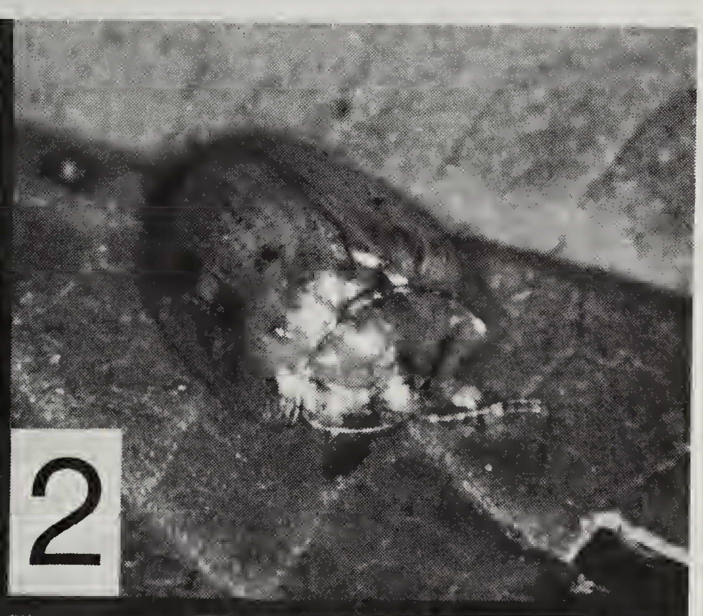
Twenty four pupae of *M. bicolor* and 19 pupae of *D. guttata,* that were all progeny of different parents, and 10 pupae of *P. clavata,* that were not all from different parents, were attached to leaves and bore masses over their dorsa. Pupae did not move their masses when pupae were touched with forceps, but the presence of masses might help to camouflage or otherwise protect them.

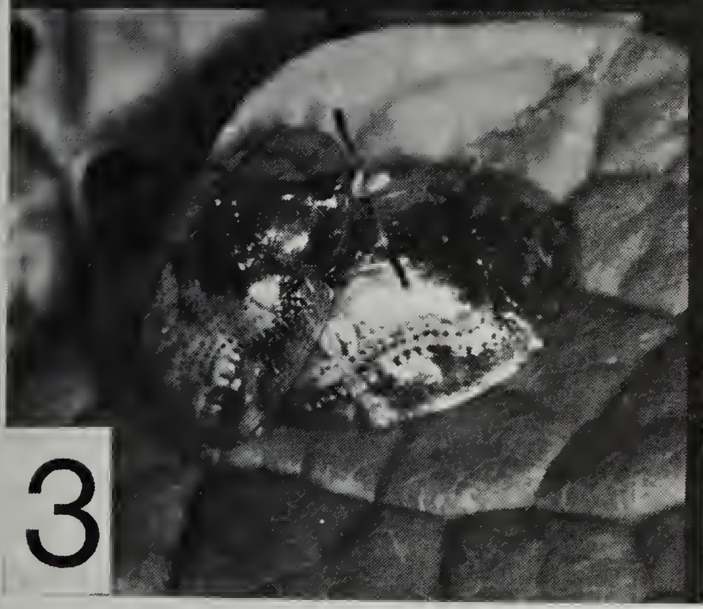
Eighteen adults of *M. bicolor* lived from 25 to 111 days (64.9, 28.56, 66.5); 5 adults of *D. guttata,* 31 to 105 days (51.9, 30.60, 42.0). One adult of *M. bicolor* was still alive at 112 days when I stopped observing it.

Fifteen *M. bicolor* adults were examined immediately after they emerged from pupae, and at this time, their upper surfaces were entirely light brownish orange. They turned to deep brownish orange with 6 black spots on their elytra in about 3 hr. One hundred and thirty four adults were examined once per day and were first observed to be entirely bright, metallic gold when they were from 14- to 27-day old adults (19.1, 2.28, 19.0) (Fig. 2 and 3). Metallic colors of another tortoise beetle, *Aspidomorpha tecta,* first occur as soon as 3 days after emergence from pupae (Neville 1977).

Fifty eight adults of *D. guttata* attained full metallic coloration when they were from 9 to 18 days old (12.1, 4.32, 13.0) (Fig. 4). Fifty randomly collected adults from the field varied in coloration. Forty eight were black with large gold markings with or without highlights of magenta, bronze, or







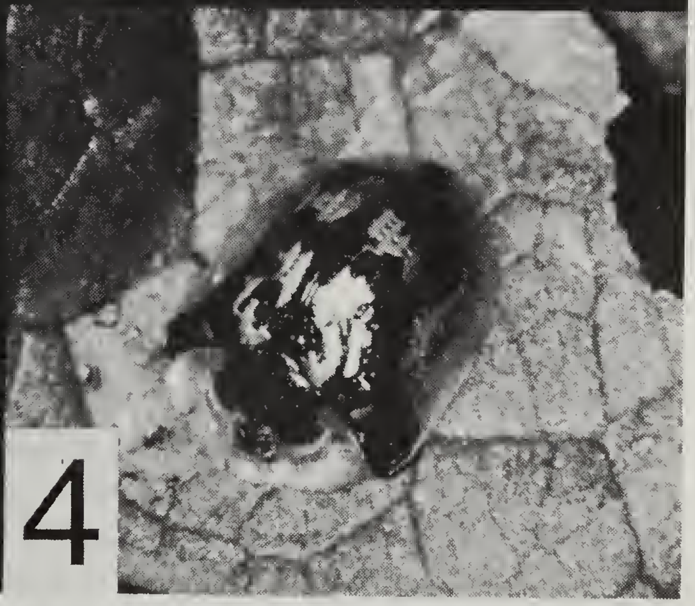


Fig. 1: Larva of *Deloyala guttata* holding four masses of exuviae and feces with its urogomphi. Fig. 2: Adult of *Metriona bicolor* in brownish-orange-with-black-dot color phase. Fig. 3: Adults of *M. bicolor* in metallic-gold color phases and *in copula.* Fig. 4: Adult of *D. guttata.*

chartreuse; one, gold and brown; and one black with very small gold markings.

Sexual behavior. Tortoise beetles were found only occasionally *in copula* in the field; therefore, mating behavior was primarily studied in the laboratory. In 3 courtships of *M. bicolor,* males approached resting females, mounted them, and antennated female heads with simultaneous or alternate antennal movements.

Six adults of *M. bicolor* were first observed to copulate when they were from 14 to 17 days old (14.7, 1.21, 14.0). Three were metallic gold; two, goldish orange with black spots; and one, bronzy gold with spots. While *in copula,* males of 19 pairs of *M. bicolor* and 7 pairs of *D. guttata* placed their forelegs on female elytral bases and middle legs on elytral midareas. Male hindlegs were on distal margins of female elytra, on leaves, in air, withdrawn against bodies, or on petri dishes, and their left hindlegs were often in different positions than right ones. Males and females held their antennae forward and spread from 30 to 180 degrees or under pronota. Several pairs of *D. guttata* and *P. clavata* were seen in linear copulation in which males and females faced opposite directions.

Pairs were first observed when they initiated copulation, or when they were already *in copula,* and thereafter they were observed once per hr for 10 hr. I assumed that pairs did not interrupt copulation between times when they were seen in copulation. Therefore, recorded mating durations are estimations and could have been almost 1 hr shorter than actual durations, and pairs may have gone in and out of copulation when I did not see them. Fourteen pairs of *M. bicolor* copulated for from approximately 180 to 583 min (338.5, 108.76, 316.5); 6 pairs of *D. guttata,* 15 to 345 min (140.0, 115.28, 120.0); one pair of *P. clavata,* 345 min.

Pairs of tortoise beetles mated repeatedly. Eighteen isolated pairs of *M. bicolor* were observed from 1 to 10 times per day for from 1 to 6 days (4.6, 2.00, 6.0), and they copulated from 1 to 6 times with the same mates (3.3, 1.44, 3.0). Seven pairs of *D. guttata* that were confined with only 1 mate were observed from 1 to 10 times per day for from 1 to 6 days, and they copulated from 1 to 5 times (2.3, 1.25, 3.0). In a polygamy experiment, 8 males and 8 females of *M. bicolor* copulated with 2 different mates, and 3 males and 3 females of *D. guttata* mated with 2 different mates. Tortoise beetle polygamy adds support to Wilson's (1975, p. 330) statement that polygamy appears to be the rule in invertebrates; adaptive reasons for this behavior are discussed by Wilson (1975) and many others.

Rapid color change in adult *M. bicolor*. Adult *M. bicolor* developed brilliant gold coloration in an average of 19 days as stated above. After they became gold, they could change to brownish orange with spots and back to gold in several min. Color transformation in indirect sunlight was from brownish orange with black spots to purplish orange with black spots to goldish orange with black spots to brilliant, metallic gold without spots. One adult did not change from goldish orange with black spots in 70 days before I discontinued observing it.

If they were not brilliant, metallic gold when they initiated copulation, *M. bicolor* usually turned this color as mating progressed. Thirty field-collected adults that were maintained in separate petri dishes for from 1 to 3 days were all placed in the same petri dish without food. Most beetles became brownish orange with black spots as they crawled in the dish. I continuously scanned the dish and as pairs commenced copulating, they were removed by urging females to crawl on leaves of *Calystegia* with prodding from a small paint brush. They did not stop copulation during this process. Pairs were transferred to separate petri dishes, and their color change behavior was observed. Two females were goldish orange at the onset of copulation, and they became gold in 152 and 360 sec after copulation initiation. One male, that was goldish orange at the onset of copulation, became gold in 232 sec, and one male that was brownish orange with black spots at the onset of copulation did not turn gold in 60 min after which I ceased observation. He might have been too young to turn gold. After the onset of copulation, 7 other females turned from brownish orange with black spots to gold in from 143 to 470 sec (253.9, 106.08, 268.0), and 7 other males turned from brownish orange with black spots to gold in from 120 to 1033 sec (367.3, 315.19, 295.0). There was no difference in speed of color change between males and females ($p < 0.05$, MWUT).

To observe *M. bicolor* change from gold to brownish orange with black spots, I held a gold beetle in my fingers and placed slight pressure on it. When its spots started appearing, I placed the beetle in a petri dish and timed its color change for 3 min. Spots started appearing in from 12 to 66 sec (39.9, 15.03, 41.5) in 14 males, faster than in 12 females which took from 26 to 141 sec (70.7, 37.53, 63.0) ($p < 0.001$, MWUT). After spots started appearing, different parts of beetles such as elytra, prothoraces, and scutella became brownish orange with a violet sheen in varying sequences among beetles (Fig. 5). Not all of these parts of particular beetles became brownish orange in 3-min periods. Usually, color change occurred symmetrically. Elytra turned orange from their lateral margins inward, and prothoracic scuta also turned orange from their margins inward. Beetles either remained still or crawled, groomed antennae, buzzed wings, and extended or withdrew antennae as they changed color.

A pilot test involved solitary, orange beetles with black spots turning to gold. I caused beetles to change from gold to orange with spots by holding them in my fingers, as described above. Four out of 10 beetles began turning gold in 10 min, and by 30 min later, some beetles periodically changed from brownish orange with spots to goldish orange and back to orange with spots. However, no beetles turned brilliant gold during 30 min.

Rapid color change in *M. bicolor* was previously reported by, e.g., Manson (1929), Swain (1948), Smith (1950), and Balsbaugh and Hays (1972). Woodruff (1976) noted that the color of this beetle varies from "brassy or greenish gold to an opalescent pinkish white sheen." In the laboratory under indirect sunlight, I found that *M. bicolor* looked brownish-, purplish-, and goldish orange, and bright metallic gold. Goldish orange might be similar to brassy gold that is reported by Woodruff. *Metriona bicolor* sometimes looked greenish gold in the field, and highlights of its coloration are probably related to reflected light from its substrate and other nearby objects. Also, depending on the inclination of the line of vision, the color varies from gold to green or even blue (Manson 1929).

Metriona bicolor, Aspidomorpha tecta (Hinton 1976), and other cassidines are evidently the only beetles that change color rapidly. Hinton (1976) reports that the colors of some cassidines are produced entirely by interference; whereas, in others, pigments modify structural colors. In *Aspidomorpha* and other genera, epidermal cells of pronota and elytra hydrate

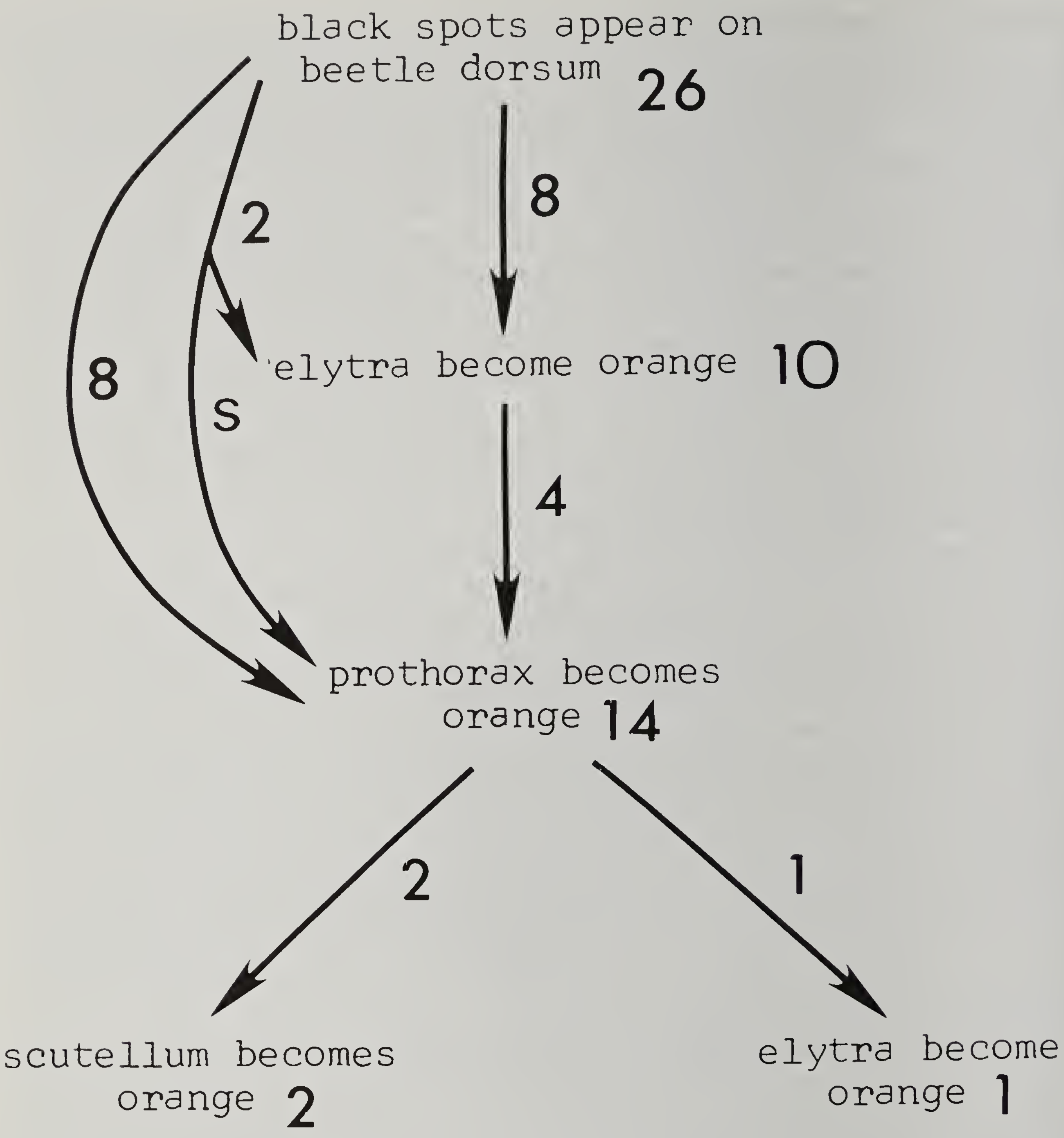

black spots appear on beetle dorsum 26
8
2
8
S
elytra become orange 10
4
prothorax becomes orange 14
2
1
scutellum becomes orange 2
elytra become orange 1

Fig. 5: Color change sequence in 26 initially gold color phase *M. bicolor* males and females after disturbance. Not all parts of all beetles became orange during the 3-min observations that were made in this experiment. The "s" denotes that in two cases, both elytra and prothoraces simultaneously became brownish-orange ("orange" in the figure).

and dehydrate integuments, and thereby alter the thicknesses of interference layers and resultant colors. Hinton further comments that no other animals are known to be able to reversibly alter interference colors.

Rapid color change in *M. bicolor* has at least 3 possible functions. First, gold adults may be difficult for birds to see when the beetles rest on sun-dappled foliage or when they reflect colors of their substrates. Similar reflecting of substrate colors may occur in some butterfly pupae (Neville 1977). Also, golden appearance of *M. bicolor* might enable them to mimic raindrops shining in the sun, as has been suggested for *A. tecta* (Neville 1977). Second, gold coloration might be a signal that they are sexually receptive because in the laboratory beetles which had not attained full gold coloration did not mate. Third, orange phase *M. bicolor* may mimic ladybird beetles (Coccinellidae). In the field on 17 June, during a 50-min search, orange ladybirds without spots (*Cycloneda munda* (Say)) outnumbered orange or gold phase *M. bicolor* on the upper sides of foliage by 17 to 3. From 1 or more meters, it was difficult for me to distinguish between orange phase *M. bicolor* and *C. munda*; perhaps insectivorous birds also have this difficulty. In the laboratory, captive, juvenile mockingbirds which had never contacted *M. bicolor* or *C. munda* apparently found *M. bicolor* palatable and *C. munda* distasteful (Barrows *et al.*, in prep.). This meager and indirect evidence suggests that *M. bicolor* are Batesian mimics of *C. munda* and perhaps other coccinellids; however, further experimentation is needed to explore this subject. The distinctive shapes of tortoise beetles may lower bird predation because inexperienced mockingbirds showed difficulty in eating tortoise beetles (Barrows *et al.*, in prep.) Regarding *A. tecta*, Hinton (1976) surmised that color change from gold to red makes beetles less conspicuous to bird predators; he did not suggest possible aposematic aspects of this color change.

ACKNOWLEDGMENTS

Richard E. White (USDA, Washington, D.C.) identified the tortoise beetles, made available his reference file on cassidines, and offered important suggestions regarding a preliminary draft of this paper. Robert D. Gordon (USDA, Washington, D.C.) identified coccinellid beetles and Theodore J. Spilman and Ashley B. Gurney (USDA, Washington, D.C.) made helpful suggestions. Janice B. Browne and Dominica Hill helped prepare the manuscript.

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